PROCEEDINGS OF THE ROYAL SOCIETY B

Proc. R. Soc. B (2006) **273**, 179–184
doi:10.1098/rspb.2005.3300
Published online 1 November 2005

Accepting loss: the temporal limits of reciprocity in brown capuchin monkeys

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Delayed reciprocity is a potentially important mechanism for cooperation to occur. It is however rarely reported among animals, possibly because it requires special skills like the ability to plan a loss. We tested six brown capuchin monkeys (*Cebus apella*) in such skills. Subjects were studied in exchange tasks in which they had to retain a food item for a given time lag before returning it to an experimenter and obtaining a more desirable reward. Experiments showed that the subjects could wait for several minutes when allowed to return only part of the initial item. When required to return the full item intact, however, most subjects could not sustain a time lag longer than 10 s. Although the duration of waiting increased with the amount of return expected by subjects, in most cases it did not extend beyond 20 s even when the eperimenter offered a food amount 40 fold the initial item. The failure of capuchin monkeys to sustain long-lasting waiting periods may be explained by limited self-control abilities. This would prevent them achieving reciprocal altruism.

Keywords: reciprocal altruism; exchange; economics; self-control; primates; *Cebus apella*

1. INTRODUCTION

As initially formulated by Trivers (1971), reciprocal altruism is a potentially important mechanism for the emergence of cooperation between unrelated individuals. To qualify as reciprocal altruism, a behaviour should be costly to the donor and beneficial to the recipient, and donor and recipient should alternate their roles, thus relying on delayed reciprocity. Despite a great deal of research, however, evidence of reciprocal altruism remains slim among animals (Pusey and Packer 1997; Hammerstein 2003; Stevens & Hauser 2004). Several studies have shown that unrelated individuals may benefit from each other's behaviour (Packer 1977; Seyfarth & Cheney 1984; Wilkinson 1984; Milinski 1987; de Waal 1989; Mitani & Watts 2001). Nonetheless, these results may be interpreted without assuming that individuals keep track of the costs and benefits of their acts. Various mechanisms may maintain cooperation in an indirect way (Dugatkin 1997; Noë *et al.* 2001). In non-human primates, in particular, it has been shown that delayed reciprocity may arise as an incidental outcome of the selfish behaviour of individuals (Bercovitch 1988; Noë 1990; Hemelrijk 1996), a mechanism known as 'by-product mutualism' (West-Eberhard 1975). It was also proposed that individuals score their partners according to their social disposition and behave accordingly with them, a process named 'attitudinal reciprocity', which does not involve any mental record of social credits and debits (de Waal 1997, 2000; Hauser *et al.* 2003).

In view of the pervasiveness of reciprocal altruism in human cooperation, its rarity in animals had led Stevens & Hauser (2004) to suggest that the cognitive prerequisites for its occurrence have been underestimated. Delayed reciprocity needs anticipation and memory abilities, it also brings into play the estimation of commodities given and received, the detection and prevention of cheating, and the ability to delay gratification. A basic component of delayed reciprocity is the ability of individuals to wait for a return. As stressed by Trivers (1971),

> The time lag is the crucial factor, for it means that only under highly specialized circumstances can the altruist be reasonably guaranteed that the causal chain he initiates with his altruistic act will eventually return to him.
>
> (Trivers 1971 p. 39)

Calculation additionally implies that the temporal dimension of reciprocity extends to the period preceding the gift. Not only should the donor foresee the conditions of return, it must also plan the initial loss and accept it.

While it is difficult to appreciate the expectations of an animal about to give a service to another in the social context, laboratory experiments allow the investigation of the goals of an individual who gives an object. Studies in brown capuchin monkeys (*Cebus apella*) and chimpanzees (*Pan troglodytes*) have demonstrated that they readily engage in exchanges with human experimenters, creating situations in which we may examine the relative values of given and received objects. Subjects can give food to receive another food that is quantitatively or qualitatively more desirable (Lefebvre 1982; Westergaard *et al.* 2004; Drapier *et al.* 2005). They may also give non-edible tokens to the experimenter in return for food (Wolfe 1936; Westergaard *et al.* 1998; Hyatt & Hopkins 1998; Brosnan & de Waal 2004*a*, 2005). Individuals may learn the use of tokens from conspecifics (Sousa *et al.* 2003; Brosnan & de Waal 2004*b*) and chimpanzees even store tokens used

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The electronic supplementary material is available at http://dx.doi.org/10.1098/rspb.2005.3300 or via http://www.journals.royalsoc.ac.uk.

Received 24 June 2005
Accepted 19 August 2005

to obtain rewards (Wolfe 1936; Sousa & Matsuzawa 2001). Some studies additionally indicate that food transfers may occur between conspecifics, but most exchanges remain indirect, that is, an individual collects pieces of food that another has dropped (Paquette 1992; de Waal 1997, 2000; Westergaard & Suomi 1997). Chimpanzees tutored in a symbol-based language, however, can request a tool from another and give him food in exchange (Savage-Rumbaugh *et al.* 1978).

Several studies have demonstrated that non-human primates postpone immediate rewards for the sake of future rewards in reinforced tasks. Chimpanzees may delay gratification for at least 3 min (Beran *et al.* 1999; Beran 2002). Macaques may also wait several seconds for a more valued reward (*Macaca fascicularis*, Tobin *et al.* 1996; *Macaca mulatta*, Szalda-Petree *et al.* 2004), but delay periods over 6 s were not tested. Until now exchanges between animals and humans were conducted on an immediate basis. When the initial reward was a food item, either it was placed on the floor beforehand or it was received, and then held by the subject for a few seconds before being returned (Lefebvre 1982; Westergaard *et al.* 2004; Drapier *et al.* 2005). In both cases the subject took the initial food item for a few seconds, yet we cannot assert that he had planned to give back such a costly item. The same may be said for the use of tokens. While capuchin monkeys exchange tokens at longer delays compared to food items, tokens are inedible by definition. Although subjects learn to associate them with a given value, they lose nothing of intrinsic value when returning tokens for food.

Accepting loss is necessary for delayed reciprocity to occur. A way to assess the anticipation of food loss is to measure for how long individuals can retain a food reward before giving it back to an experimenter. In order to test the ability of brown capuchin monkeys to delay returns, we designed two series of experiments, where the individuals had to exchange food on a qualitative basis and then on a quantitative basis. The results provide evidence that capuchin monkeys can foresee gains and losses, but that their ability to sustain significant losses is limited, even when expected gains are sizeable.

2. GENERAL METHODS

(a) *Subjects and conditions*

We tested six brown capuchin monkeys: one female (Aso 14 years old at the start of the study) and five males (Clo 12, Bib 9, Acc 7, Arn 5, Pis 4). They belonged to a social group of 20 individuals maintained at the Primate Center of the Louis Pasteur University, Strasbourg. The animals were housed in an enclosure composed of two indoor compartments (33 m^2 total) and four outdoor wire-mesh compartments (45 m^2 total), 3 m high. Commercial monkey diet and water were available *ad libitum* in the indoor rooms. Subjects were never deprived of food. Compartments were connected by sliding doors. For testing, subjects were individually separated from the rest of the group in an outdoor compartment.

(b) *Testing procedure*

Subjects had been trained to exchange food items with a human experimenter in a prior study (Drapier *et al.* 2005). For testing, we separated a subject from the others in an outdoor compartment. The experimenter stood in front of the wire mesh with one food item in each hand and showed them to the subject for 5 s. Then she gave one item to the subject. After a given time period, the experimenter held out the empty hand while showing the second item on the other hand. If the subject gave back the first item by putting it in the experimenter's hand, he was allowed to take the second item. If the subject did not give back the first item, the experimenter gave nothing and the trial ended. The experimenter randomly changed hands to present the items. The experimenter waited for 30 s after which the subject ended food consumption before starting another exchange. We ran the subjects in one or two test sessions per day. In the latter case, sessions were separated by an interval of at least 2 h. The food items presented to subjects were monkey diet pellets, sweet biscuits and carrots. When given the choice, subjects preferred carrots to pellets, and biscuits to the other two kinds of food (Drapier *et al.* 2005). Prior to experiments, we ran the subjects in a training phase in which they had to wait for 5 s before receiving a piece of biscuit when returning a piece of carrot. We required the subjects to succeed in at least 90% of trials in a session. Subjects needed between 5 and 8 sessions of 12 trials to reach the criterion.

(c) *Statistics*

The dependent variable was the percentage of returns over the total number of trials in each phase or session. We used non-parametric statistics, the Wilcoxon matched-pairs test and the Friedman ANOVA, two-tailed (Siegel & Castellan 1988). The significance level was set at 0.05. Average values are given as means and s.e.m.

3. FIRST SERIES OF EXPERIMENTS: TESTING WAITING TIME IN QUALITATIVE EXCHANGES

(a) *Experiment 1a*

We designed experiment 1a to test whether the duration of the waiting period could vary according to the relative value of the food pieces being exchanged.

On each trial, the experimenter first offered either a pellet or a piece of carrot, then offered a biscuit to the subject. The food was presented in pieces of $1 \times 2 \times 0.5$ cm. Once a subject received the first item, he had to wait for periods of variable durations before the experimenter presented a second item. We ran the subjects in a succession of experimental phases, which differed by the time lag tested: 10, 20, 40, 80, 160, 320, 640 s. The time lag increased from one phase to the next. Each experimental phase was composed of four identical test sessions of 12 trials each. In a test session, there were 4×3 trials presented in random order and differing by a combination of two factors: the nature of the food item first given (six trials with a pellet, six trials with a piece of carrot) and the time lag (six trials of 5 s duration, six trials corresponding to the studied time lag). We carried out tests of 5 s time lags to ensure that the subjects be rewarded throughout the experiments and displayed a persistent willingness to participate in the experiments; at this duration, the subjects exchanged at a success percentage of 96.3 ± 0.3 during the whole experiment.

For each time-lag condition, we used a Wilcoxon test to compare the subjects' percentages of return according to the value of the food items to be returned. The results showed that individuals displayed lower success rates

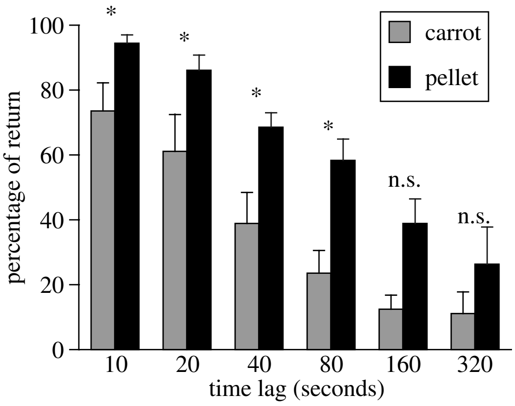

Figure 1. Percentage of return according to the value of the food item (pellet or carrot) to be returned to obtain a piece of biscuit (Wilcoxon test, $N=6$, $*p<0.05$) in each time-lag condition.

when they had to return a piece of carrot compared to a pellet (figure 1). The return percentage decreased as the time lag increased. At 320 s, four subjects failed to return any carrot and we stopped testing them. We tested the other two subjects (Ass, Arn) at 640 s, their performances dropped to 0 for carrots but they still returned pellets at a rate of 58.3 and 91.7%, respectively. It should be added that subjects often nibbled the piece of food before returning it to the experimenter (percentages relative to the number of trials in which the food was nibbled: $47.5\pm9.8\%$ for pellets and $95.8\pm2.4\%$ for carrots; amount of food returned in exchanges: $51.0\pm10.4\%$ for pellets and $13.3\pm6.1\%$ for carrots).

(b) *Experiment 1b*

In experiment 1a, the fact that the subjects were allowed to return an item after having possibly consumed part of it could have affected the rates of exchange. In experiment 1b, we required the subjects to return the first item intact.

In each trial, the experimenter first offered a piece of carrot, then offered a biscuit to the subject. If the subject put the carrot to its lips, he did not receive the biscuit. The food was presented in pieces of $1\times2\times0.5$ cm. We first submitted the subjects to a training phase in which they received a piece of biscuit only when they had returned a piece of carrot intact. There was no time lag. We required the subjects to succeed in this task during six consecutive trials. All subjects reached this criterion in one or two sessions of 12 trials. We then ran the subjects in a succession of experimental phases composed of one to three identical sessions. Each session was composed of 12 trials presented in random order: six trials without time lag to keep the subjects willing to participate in the experiments and six trials with the tested time lag (2, 5, 10, 20, 40 s). The time lag increased from one experimental phase to the next. When a subject succeeded in at least 75% of exchanges in a session, he was submitted to the next phase. When a subject failed to reach this threshold, we ran him in a further session of the same time lag. If a subject failed to reach a 15% threshold after three sessions, we stopped testing him. If a subject obtained between 15 and 75% of success after three sessions, he was submitted to the next time lag in a last experimental phase. The numbers provided below are those obtained in the last session of each phase. When there was no time lag, the subjects displayed 100% success.

The results showed that three subjects did not succeed in the task, they had a return percentage of 4.2 ± 4.2 at a 2 s time lag. The other three subjects displayed high return percentages at 2 s (90.3 ± 1.4), 5 s (88.9 ± 5.0) and 10 s (60.4 ± 17.4). Their performances were lower at 20 s (25.0 ± 17.3) and approached 0 at 40 s (2.1 ± 2.1 for the two subjects tested) (cf. electronic supplementary material for full results).

4. SECOND SERIES OF EXPERIMENTS: TESTING WAITING TIME IN QUANTITATIVE EXCHANGES

(a) *Experiment 2a*

In experiment 1b, a relatively weak difference of palatability between the first and the second item might explain the short delay sustained by subjects. We then conducted exchange tasks on a quantitative basis to better appreciate the subjects' costs and benefits.

We first submitted the subjects to a training phase in which they had to return a piece of biscuit intact to receive a piece of biscuit four times the size of the first. The time lag was set at 2 s. We required the subjects to succeed in this task during six consecutive trials. All subjects reached this criterion in three to seven sessions of 12 trials. The procedure was then identical to those of experiment 1b except that the experimenter first offered a piece of biscuit of $1\times2\times0.5$ cm, then presented to the subject another piece of $2\times4\times0.5$ cm. When there was no time lag, the subjects displayed 100% success.

The results showed that the return percentage of the six subjects was 90.3 ± 2.3 at 2 s and 70.2 ± 13.3 at 5 s. Five subjects exchanged in the 10 s time lag phase but their return percentage decreased to 48.3 ± 18.1. Three subjects were still tested decreased to a 20 s time lag but their performances approached zero (1.4 ± 1.4) (cf. electronic supplementary material for full results).

(b) *Experiment 2b*

In experiment 2a, the short duration of the waiting period could be related to a limited difference between the quantity returned and that eventually received. We designed experiment 2b to test whether the subjects could postpone pay-off according to the amount of food expected.

There was no training period. We ran the subjects in a succession of phases composed of four sessions each. Each phase differed by the time lag tested: 2, 5, 10, 20, 40 s. In each trial, the experimenter first offered a piece of biscuit of $1\times2\times0.5$ cm, then presented to the subject a piece of another size: $2\times2\times0.5$ cm (twice the size of the first offered item), $2\times4\times0.5$ cm (four times) or $4\times4\times0.5$ cm (eight times). Each session was composed of 12 trials, in which each of the three possible sizes was presented four times in random order.

For each time-lag condition, we used a Friedman test to compare the subjects' performances for the three different proportions of biscuit exchanged against the initial piece of biscuit. The results showed that the subjects' waiting periods increased with the size of the piece of biscuit returned (figure 2*a*). At 20 s, the return percentages of four subjects dropped to 0, and the other two subjects (Acc, Bib) returned the piece of biscuit at low rates.

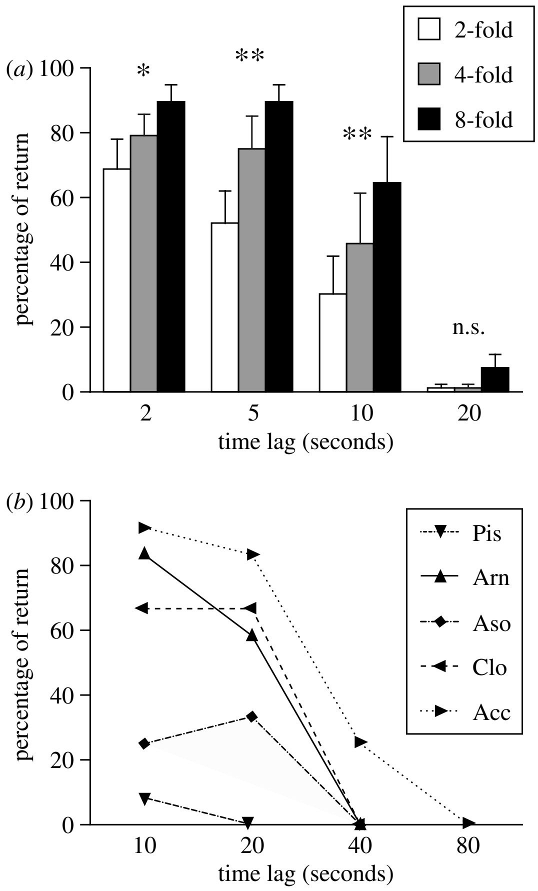

Figure 2. Percentage of return according the food amount secondarily given to the subject in each time-lag condition: (*a*) Experiment 2b: mean scores for three different proportions of biscuit exchanged against the initial piece of biscuit (Friedman test, $N=6$, $*p<0.05$, $**p<0.01$). (*b*) Experiment 2c: individual scores of five subjects when food amount is 40 times the size of the initial piece.

At 40 s, the performances of the latter two subjects dropped to 0.

(c) *Experiment 2c*

The time lag sustained by the subjects remained limited in experiment 2b. It could be that the subjects estimated that the pay-off was not worth the wait, hence devaluing future rewards. In experiment 2c we considerably increased the subjects' gains to assess the maximal waiting period which they were able to maintain.

There was no training period. In each trial, the experimenter first offered a piece of biscuit of $2\times1\times0.5$ cm, then offered to the subject five pieces of $4\times4\times0.5$ cm, i.e. the subject received an amount of biscuit 40 times the size of the initial item. To account for the large amount of food possibly obtained by the subjects, we reduced sessions to two daily trials. If the subject succeeded in the first trial, the second trial occurred 20 min after the end of food consumption. Each subject was run in successive six-session phases that differed by the time lag tested: 10, 20, 40 and 80 s. The time lag increased from one phase to the next. When a subject's performances dropped to 0%, we stopped testing him. For reasons irrelevant to the study, one of the six subjects (Bib) could not be tested.

The results showed that four out of five subjects were able to wait 20 s before returning the food item, but three of them failed to return it at 40 s (figure 2*b*). A single subject still returned the food item in 25% of trials at 40 s, but he stopped exchanging at 80 s.

5. DISCUSSION

The results of experiment 1a confirmed that brown capuchin monkeys maximize pay-offs when requested to return food on a qualitative basis (cf. Westergaard *et al.* 2004; Drapier *et al.* 2005). We additionally found that subjects could wait for several minutes before returning food. They waited for longer time periods when they had to return a low-value food in comparison to a better-valued food. It must be stressed, however, that the nature of the exchange could have been altered in two different ways. First, the subjects often nibbled the initial food item and returned only part of it. Second, the pellets were of quite a limited value to the subjects, since they were available *ad libitum* just before the time of experiment. The cost represented by the giving of pellets was thus questionable. In experiment 1b, we required the subjects not to nibble the original item before returning it. As a consequence the subjects' performances decreased. Whereas in experiment 1a subjects exchanged a piece of carrot for a piece of biscuit after a time lag of several minutes, in experiment 1b most performances dropped under a 10 s interval. The time necessary to nibble and eat the piece of food could not account for such a discrepancy, since these actions usually lasted less than a dozen seconds.

It has been asked whether animals can anticipate the consequences of their choices (Roberts 2002). The long waiting period found in experiment 1a demonstrates that capuchin monkeys may to some extent plan future events, which is consistent with the anticipation performances reported in the species (Fragaszy *et al.* 2004*a*). In a task where subjects have variable chances of obtaining rewards, they may decide to work or not according to their expectations of success (de Waal & Davis 2003). Capuchin monkeys may perform several exchanges in succession to obtain a final reward, they use tools sequentially to achieve a goal, they even transport tools to a food reward site (Westergaard & Suomi 1994; Westergaard *et al.* 1998, 2004; Cleveland *et al.* 2004; Drapier *et al.* 2005). However, the goal-directed behaviours tested in the laboratory did not exceed a time scale measured in seconds. In the forest, capuchin monkeys travel in straight lines between food sites spaced 200 m apart (Janson 1998) and there are hints that individuals are able to transport pounding stones similar distances to crack nuts at anvil sites (Fragaszy *et al.* 2004*b*).

In view of the goal-directed behaviours displayed by capuchin monkeys, the duration of the waiting period sustained by the subjects when required to return an intact food item appears limited. The short time lag observed in experiment 1b might have been due to a weak difference of palatability between the two food items offered to subjects. To raise the stakes in a measurable way, we then tested the subjects in exchange tasks based on different quantities of food. In experiment 2a, subjects could obtain an amount of food four times the size of the initial piece. The results showed that the longest waiting periods sustained by the subjects ranged between 5 and 10 s. By offering rewards of different sizes in experiment 2b, we further demonstrated that the duration of waiting periods increased with the amount of return expected by subjects, but once again the time lag did not exceed 10 s in most instances. (It may be worth mentioning that contrary to previous experiments we did not add trials with short time lag or no time lag in experiment 2b. The consistency of the results of experiments 1b and 2b indicated that receiving a reward with limited waiting cost did not affect the motivation of capuchin monkeys to wait for longer delays in a session.) As a last step, we dramatically increased food return in experiment 2c. When subjects were offered an amount 40 times the size of the initial one, most of them proved to be able not to eat the initial item until 20 s on several occasions, yet their performances dropped to zero at a delay of 40 s. Only a single subject could wait for 40 s in a few instances. In short, experiments consistently showed that the subjects tested could readily avoid consuming an attractive food item until 10 s, but that waiting for more than 20 s was beyond their normal range of response.

There is more than memory and anticipation in the temporal dimension of exchanges. Studies on humans and animals have shown that individuals rapidly discount the value of delayed rewards (Mazur 1987; Rachlin *et al.* 1991; Green *et al.* 1994, 1995; Richards *et al.* 1997; Baker & Rachlin 2002). One might argue that the limited time lag sustained by capuchin monkeys before return was an effect of the devaluing of future benefits (cf. Stevens & Hauser 2004). When we provided subjects with pay-offs as great as 40 times the initial reward, however, they generally could not wait for more than 20 s, making the temporal discounting hypothesis implausible. We propose alternatively that the failure of capuchin monkeys to sustain long-lasting delays was a consequence of their limited self-control abilities. By human standards, capuchin monkeys appear to be impulsive animals. When tested in cognitive tasks and tool-use, for instance, their main way of solving problems is to attempt any combination of objects and actions (Fragaszy *et al.* 2004*a*). In the exchange task, subjects had to overcome their tendency to eat food. Although they could anticipate the reward, they were unable to accept the loss of food and suppress their consummatory response beyond a relatively short time scale. As a result, the subjects' tendency to avoid a loss was stronger than their tendency to obtain a reward. Such 'loss aversion' is a basic component of human transactions (Rabin 1998). Following Mischel (1974), we may envision two behavioural stages in the subjects' planning: first deciding whether or not to return the food item, and second facing the delay interval and waiting for the opportunity to return the item. The fact that subjects held the item while waiting may have heightened the difficulty in bridging the interval. Studies on delay gratification in children and pigeons showed that subjects could wait longer when the reward was not present (Mischel 1974; Grosch & Neuringer 1981), but such an effect was not consistently found for chimpanzees (Beran *et al.* 1999; but cf. Boysen & Berntson 1995).

Despite the small number of subjects, the present findings have important implications for the occurrence of delayed reciprocity among animals. If the short time horizon at which capuchin monkeys can accept a loss comes to be a general finding, that would help understand the lack of evidence regarding reciprocal altruism in nature. At the evolutionary level, reciprocating at a scale of a few dozen seconds would qualify as mutualism rather than reciprocal altruism. To get further insights on the basis of exchanged acts, we need comparative data about the duration of the waiting periods that individuals from different species could overcome to return some food against a larger amount of food. Admittedly, giving goods might be more difficult than giving services. However, even services must be costly to qualify exchanges as reciprocal altruism. Knowing whether animals would wait for seconds, minutes or hours before returning goods would shed light on their abilities to reciprocate in social interchanges. From the performances observed in chimpanzees in exchange and cognition tasks, for instance (e.g. Savage-Rumbaugh *et al.* 1978; de Waal 1989; Hyatt & Hopkins 1998; Beran *et al.* 1999; Mitani & Watts 2001; Beran 2002), we may expect that great apes may postpone returns on a longer time scale than capuchin monkeys.

The authors are grateful to P. Uhlrich, C. Eschbach, R. Gabarre, N. Guen, P. A. Lydoire, A. Malo and A. Sternalski for assistance with experiments, and A. M. Ducoing for language advice.

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